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THE NATURALIST'S OCCUPATION:

1. GENERAL SURVEY.

2. A SPECIAL PROBLEM.

BY

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SECOND LECTURE.

THE NATURALIST'S OCCUPATION.¹

By C. O. WHITMAN.

I. *General Survey.*

I SCARCELY need remind you that the domain of Biology is a broad one, and that it has long since become impossible for one person to master the different provinces of knowledge embraced in it. The most that I can hope to do, is to take you into one small section of the great realm of life, and try to give you an inside view of some of the problems now occupying attention.

As this many-sided occupation may be approached with almost equal advantage along any one of many intersecting paths, a hasty general survey may be the best means of getting the points of the compass.

Let us take systematic biology as our starting point, and from this as a centre find our way into the other provinces of biology, with a view to understanding their general features and relative positions.

What is the chief end to be reached in the classification of plants and animals? The general drift of bio-

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logical research is in the direction of a *genealogical* system of classification — a system based upon, and expressing, the kinship which underlies the whole organic world. From this standpoint, the myriad forms of organisms that have arisen since the dawn of life, genealogically arranged and viewed as a whole, would present the branching figure of a tree. The trunk and branches of this great tree, representing ancestral forms, have been buried in the sand and mud of geologic ages, and preserved only as an imperfect fossil frame-work, so that we see only the terminal buds of its topmost twigs in the plants and animals of to-day. To trace out and reconstruct such a tree is a work of magnitude, scarcely dreamed of in the philosophy of cabinet naturalists. The best classification within the range of present possibilities can only have a tentative value. It can have not a single hour's security against the invasion of newly discovered facts — an invasion that is advancing along a thousand lines with plenary authority to spare nothing fictitious. The goal of systematic botany and zoology is not then the terminus of any one line of research, but rather a focal point of all the biological sciences.

Having noted the principal aim of classification, we have now to glance at its position, scope, and functions. The low standards followed by many systematic writers have brought reproach upon this department of knowledge; but the reproach is certainly misplaced, and we must accord to systematic biology the high position to which its true aims and functions entitle it. Its first business, obviously, is to ascertain what forms of life now exist, and to describe, name, and catalogue them

for the purposes of easy and certain identification. Although much of this work can have only a provisional value, it is, nevertheless, quite indispensable ; for there is not a single department of biology that does not continually profit by its acquisitions, nor indeed is there one that can make any great progress without its aid.

The process of coining names and labelling new species must continue for a long time to come ; but, it does not of course follow, because systematic names are indispensable, that we can profitably spend our time in committing them to memory. That is the delusion of inexperience and the conceit of charlatanism. Time was when the knowledge of a thousand names secured one the title of botanist or zoologist, and when the capacity for ten times that number was esteemed the measure of a great naturalist ; but if we may believe a celebrated German botanist, Schleiden, such qualifications fell below par more than half a century ago.

In the beginner, and in the general observer, we frequently meet with a superstitious regard for names that blinds them to the real character and aims of natural history. With them, an ideal naturalist is supposed to have an encyclopedic knowledge of names, and to be ready for any worm, beetle, or butterfly, that may be laid before him. If he has the courage to say he does not know the name of the form presented, the inquirer is amazed at the confession of ignorance ; if a vernacular name is offered, the information is received with evident disappointment ; but if some unintelligible, polysyllabic, cacophonous Greek or Latin compound is glibly

enunciated, the awe-stricken recipient retires, feeling profoundly edified, and credits his informer with having fulfilled the function of a great naturalist. This mischievous delusion is too often encouraged by those who are able and willing to impose upon it, or who have not the courage to follow the injunction so often given by Professor Agassiz at Penikese, — “Learn to say you do not know.”

Pitiable as is this fear of appearing ignorant, and despicable as is the impostor’s pretence of knowledge, there is no ground in either for prejudice against systematic names.

Whoever reflects on what the binary nomenclature, introduced by Linné, has done for zoology and botany, will scarcely need to be told that no misuses, excesses, or abuses to which systematic work is liable, can detract from its importance. Indeed, it may be said that time will increase rather than diminish the value of such work. Thirty years ago our systematic names stood for differences and resemblances, the deeper significance of which had only been caught by Darwin and Wallace. The idea of the genetic unity of the organic world set the whole field of systematic work in a blaze of light, imparting to it an interest and a dignity of the highest order.

The second important function of systematic biology is to arrange its forms in a genealogical system. But for the fulfilment of this function, systematic biology requires the aid of all the sister branches of knowledge, and in return renders the important service of recording their verdicts along with its own. The record, representing as nearly as possible the consensus of all the mor-

phological and physiological sciences, shows how far the reconstruction of the tree of life has been carried, and thus furnishes a chart which is invaluable as a guide in the selection of subjects for investigation.

When the classifier, or taxonomist as he is sometimes called, has taken account of morphological features, modes of reproduction, habits, instincts, and distribution, he has exhausted the resources of his special province. The conclusions reached and the questions raised are then to be submitted to other departments for revision and further investigation.

Let us suppose that the preliminary work of naming and describing has been completed, and that the taxonomist undertakes with purely descriptive data to map out the genealogical tree. With superficial characters alone, it is evident that he could not advance very far, although, according to the supposition, he would have the immense advantage of knowing precisely what the task is. What such an advantage means, becomes clear when we remember that, with all the light of all the sciences, we waited until the last half of the nineteenth century for the formulation of the problem. With this key to the situation, a quarter of a century has outdone the blind plodding of all previous centuries, and the old landmarks have been left with a speed that threatens to make Rip Van Winkles of us all. Armed with such an advantage, the investigator would certainly be able to find in external characters important clews to genetic relationships. But if limited to those methods and means which naturally belong to surface observation, he would remain in absolute ignorance of a great part of the animate world, and would be utterly powerless to discover in

what the bond of unity actually lies. He would have no conception of what Huxley has called "the physical basis of life," and the structural unit of all organisms would lie wholly beyond the range of his perception. That isthmus of small life between the animal and vegetable kingdoms, his unaided vision would never discover. In searching for intermediate forms, he would inevitably be led astray by those deceptive appearances under which adaptive development and degeneration have concealed so many ancestral relationships. Sessile animals, like the sponges, the hydroid polyps, the sea-anemones, the polyzoa or moss polyps, the ascidians, and many others from the higher as well as the lower classes, would be separated from animals having the power of locomotion, and be regarded either as plants, or as forms representing both plants and animals. Where immobility is combined with the branching form, as in the hydroid polyps, the disguise would be complete. Even Linné, the great lawgiver in systematic biology, described such forms in the tenth edition of his "*Systema Naturæ*" as "plants with animal flowers"; and in the twelfth edition, which concluded his systematic work, he held to the opinion that the stock of the hydroid colony is a true plant, while its "flowers" are true animals. This idea was embodied in the word zoophytes, plant-animals, a word that has done varied service in systematic zoology from the middle of the 16th century.

The utter insufficiency of external characters as a guide to genetic affinity, is well seen when we come to such forms as the so-called compound ascidians, which are found encrusting the rocks along the shore. At first sight one would not even detect any signs of life here,

and appearances would suggest relationship to the lichens sooner than to the vertebrates. If we cut open the fleshy encrustation, and examine under the microscope the contents of some of the little sacks found in it, we discover some minute tadpole-like beings, representing the larvæ of the ascidian. The structure of these remarkable creatures repeats the fundamental features of the vertebrates so perfectly that we are compelled to place them in the same great family. They have a chordal axis with a nerve-tube on one side and the alimentary tube on the opposite, with gill-slits perforating the throat, features common to all vertebrates in early life. Although the adult ascidian bears not the remotest resemblance to a vertebrate, the combination of these characters in its larva proves that it belongs to the vertebrate stock. The larva reaches the adult condition by a process of degeneration. It fixes itself to a stone by its head, then loses its tail, its only organ of locomotion, and sinks into a purely vegetative existence. So completely are its original features obliterated, that its vertebrate nature would never have been suspected, had not embryology brought to light its developmental history. The striking agreement with the development of the curious worm-like fish, *Amphioxus*, as made known by Kowalevsky, a Russian embryologist, led Professor Haeckel of Jena to regard the ascidian as the ancestor of the vertebrate stock. Startling as such a proposition was, it was favorably received at first, and was approved, though with reserve, by no less a logical and critical thinker than Huxley. Most authorities now concur with Lankester and Dohrn in regarding both *Amphioxus* and the ascidian as our degenerate vertebrate cousins.

Thus you see how far from the surface the truth may lie, and how, in the systematic position of a single form, we may find a problem which only yields to solution after exhausting the resources of nearly every department of animal biology.

In order to correct and extend the results of surface observation, the investigator appeals first to internal structure, and is thus led into the province of anatomy. Here fundamental features of relationship are brought more clearly into view; and, following the general law that animals or plants of like structure have descended from common ancestors, it becomes possible to outline, in a rough way, a genealogical system. It is here that the investigator would begin to grasp the meaning of those deeper resemblances, called homologies, and learn to distinguish between these and deceptive analogies. But nature has concealed many of her more important homologies under disguises that a study of adult structure could not penetrate. Comparative anatomy, in the hands of such men as George Cuvier, Friedrich Meckel, Johannes Müller, Richard Owen, Thomas Huxley, and Carl Gegenbaur, has accomplished wonders in this direction, but it owes many of its greatest discoveries to the aid of embryology and paleontology. Its greatest achievement was the reduction of the animal world to four great types, and the same high elevation was reached independently by comparative embryology.

But the type system of George Cuvier and Carl Ernst von Baer did not finish the reconstruction of the genealogical tree; for it failed to grasp the full meaning of like development and like structure. Comparative anatomy

found ascending grades of organization in the vertebrates of the present; paleontology discovered a corresponding gradation in the vertebrates of the past; and embryology revealed the same serial gradation in developmental stages. The discovery of this most remarkable parallelism between the three series, the anatomical, the paleontological, and the embryological, is one of the most brilliant in the whole history of biology, and one which with pride and admiration we place to the credit and honor of Louis Agassiz. It is remarkable that these three of the leading biologists of the century, after laying the foundation of the theory of transformation, remained to the end its most determined opponents. It was left for Charles Darwin to show that the coincidence pointed out by Agassiz between the geological succession, the embryonic development, and the zoological gradation, held also in the geographical distribution of animals in the past and the present, and to find the interpretation of the fact now universally accepted.

The recognition of so fundamental a truth as that of community of descent, at once raised every department of biology to a new plane, gave new aims to each, and profoundly altered their relations to each other. Descent was seen to be "the hidden bond of connection" so long sought for under the "natural system" of classification. Embryonic development came to be regarded as the epitomized history of ancestral development. As Darwin puts it, the embryo is "a picture, more or less obscured, of the progenitor, either in its adult or larval state, of all the members of the same great class."

"In two or more groups of animals, however much they may differ from each other in structure and habits

in their adult condition, if they pass through closely similar embryonic stages, we may feel assured that they are all descended from one parent-form." Thus embryology came to have a higher value in classification than anatomy, and to take the place assigned to it by v. Baer more than half a century ago, as "the true torch-bearer in the investigation of organic bodies."

Embryology and paleontology have become complementary sciences, associated in the common aim of determining the genesis and the history of life. The peculiar charm of embryology is, that it brings us into direct contact with living forms, places us face to face with the phenomena of life, and reveals in the history of the individual the principal events in the history of the race. It holds the key to many a problem that has exhausted the resources of all the sister branches of biology, and promises to contribute more than all the rest towards the solution of the great mystery of life.

In order to illustrate the relative position of embryology, and at the same time the nature of the naturalist's work, let us now look at one of the problems before him.

II. *A Special Problem.*

Naturalists are familiar with the efforts of comparative anatomy to determine the number of segments in the vertebrate head. At the beginning of this century, Germany's great poet, Goethe, and one of her most gifted naturalists, Oken, came independently to the idea that the skull is only an enlarged and otherwise modified portion of the backbone ; that is, that it is composed of

a number of segments, each of which is the structural equivalent of a vertebra. The idea was suggested by the sutural lines in the mammalian skull, which appeared to mark the boundaries of successive segments. Thus arose the so-called "vertebral theory" of the skull, which was widely accepted and which was made the corner stone of Richard Owen's great work on the comparative anatomy of vertebrates. If the skull could be regarded as three, four, or more modified vertebræ, it followed that the brain might be considered as a portion of the spinal column, and that the cranial nerves were the equivalents of the spinal nerves. It was impossible to settle these questions by compitative anatomy, and the assistance of embryology was invoked. The discovery by Jacobson, that the bony skull is preceded in development by a so-called "*primordial cranium*," consisting of a cartilaginous case, which, although a direct continuation of the cartilaginous basis of the backbone, yet differs from it in not being divided into segments, and the fact that the adult skull is really a *double* brain case, the inner portion representing the primordial cranium and its derivatives, or by bone that has replaced it, while the outer portion consists of the so-called *dermal bones* that have been added externally and secondarily, have been used with great force by Huxley, against the vertebral theory of the skull. If the skull ever consisted of segments comparable with the vertebræ, the proof of this should appear in the primordial cranium, as it is found to-day in the lower fishes, or in the course of its development.

Since the time of Goethe and Oken, we have learned the important lesson, that the place to look for primitive

vertebrate characters is in the lower rather than the higher forms, and in the embryos rather than in the adults. The original expounders of the vertebral theory pursued just the opposite course, and were thus deceived by superficial analogies.

This theory, wide of the mark as it was in its original form, contains a germ of truth, which embryology has brought to light. Its fundamental idea, that the head, in whole or in part, is composed of segments morphologically equivalent to those of the body, may now be said to be an established fact. The problem as it now stands is this,—How far is the segmentation of the body carried forward into the head? in other words, how many segments are represented in the head? Let us look a little further into the nature of the problem, and the methods and means of approaching its solution.

The subject is a difficult one to make intelligible to those who are not familiar with the main features of development; but it is so full of instruction, that it cannot fail to yield some points of interest even to a most superficial examination. Possibly the idea of segmentation of the head, or, to use the technical expression, the metamerism of the head, may appear to some of you quite devoid of general interest or importance. The principal charm of the subject of course lies in its environment, if I may use such a term, to express its general relations or bearings. In attempting to decipher the metamerism of the vertebrate head, we are really engaged in tracing the history of the origin of the great vertebrate stock or phylum. It is simply a question of the genesis or the *phylogeny* of the vertebrate type,

at the head of which stands man himself. We do not know when nor how this metamerism of the vertebrate arose ; but, both embryology and paleontology afford ample evidence that it existed long before it took the form of vertebræ. Among the earlier and extinct forms of fishes are found some without bony vertebræ, but still divided into segments ; and in the development of the fishes and other vertebrates of to-day, we find that the vertebræ are preceded and predetermined by a primordial division of the trunk into a series of uniform segments. This division appears very early in the embryo, long before there is any cartilage or bone, and before there is any trace of limbs, or indeed of any distinctive *vertebrate* organ, except the cordal axis referred to in speaking of the ascidian larva. Now this primordial segmentation carries us back to a stage in the evolution or phylogeny of vertebrates, so full of meaning that its contemplation would seem to be enough to arouse the interest of the most worldly-minded.

This is a stage through which every vertebrate passes on its way from the egg to the adult, a stage in which the fish, the amphibian, the reptile, the bird, the beast, and man find a common level, and in which every title to superior rank lies in unexpressed potentialities. But more than this ; for it is here that the vertebrate is an invertebrate, and stands beside its prototype, the segmented worm. On the same metropolitan plain, the lobster, the crab, the insect, in short all the members of the great arthropod group, meet and acknowledge their community of descent. Thus, the great branches of the genealogical tree represented in the higher types first defined by Cuvier converge and unite in a common

stem, which bears the deep and enduring mark of metamerism.

So much for the general significance of metamerism. Let us now return to the vertebrate head. If the metamerate type of structure precedes and forms the foundation of the vertebrate type, then the question how many primordial segments are represented in the head takes precedence of the question how many vertebrae compose the skull. The inquiry takes us back to that interesting stage in which the embryo becomes divided into a chain of segments. But here we find that the transverse lines marking the boundaries of the segments do not extend into the region of the head, or at most only into its hinder portion. But we are not yet satisfied that the head is a thing *sui generis*, built upon a plan fundamentally different from that of the body. Baffled in the attempt to find *direct* evidence sufficient to demonstrate the unity of plan which we suspect underlies both the head and the trunk, we next resort to indirect or circumstantial evidence, and begin to question whether the records of ancestral development have been perfectly preserved in the embryonic development. It is here that the towering difficulties of the problem come into view, in scaling which investigation rises to its sublimest heights.

Before the division into segments, there is nothing in the embryo to show even approximately where the head ends and the body begins; the part which is destined to become the head forms with the rest a continuous whole, as shown in the external form and in the continuity of like structural elements. The cordal axis before alluded to is the precursor of the backbone, and

this structure extends through the greater part of the head region of the embryo, from which we may safely infer that, at least, so much of the primordial cranium as possesses this structure must be regarded as a direct continuation of the vertebral axis, even though no distinct outlines of segments appear in it. In the absence of such outlines, the inquiry turns upon *indications* which may betray their former existence. For evidence of this sort, the investigator continues his search, first of all, in the *posterior* region of the head, since this is demonstrably the least modified. Now it is just here that embryology has been able to demonstrate, in some of the lower fishes, the existence of at least one genuine *vertebral* segment. In a remarkable shark from Japanese waters, which Mr. Garman of Harvard has recently baptized with the name, *Chlamydoselachus anguineus*, as I learn from Dr. Ayers, who has lately studied its cranium, there are unmistakable evidences of from three to five cranial vertebræ. Indications of a considerable number of *primordial* segments, or protovertebræ as they are called, have been discovered in the hind head of the embryo of the amphibian, the reptile, the bird, and even the mammal. In the lowest representative of the fishes of to-day, the much-talked-of *Amphioxus*, the segments and the chordal axis extend from end to end; and the head merges so completely in the trunk, that the most searching examination has scarcely yet been able to fix any boundary line. Although *Amphioxus* takes an isolated position, and may have sacrificed some elements of its head in exchange for the material enjoyments of a semi-vegetative existence, still it must be admitted as

an eligible witness to the metamerism of the vertebrate head.

We are indebted mainly to recent studies on the development of the nervous system for the views now held on this subject. In the trunk we find each segment provided with a pair of so-called spinal nerves, both of which spring from the spinal cord by two short roots, known as the anterior and the posterior root. The posterior root bears, just before its union with the anterior root, a spinal ganglion, and is thus stamped as something different from its fellow. This anatomical distinction is the basis of a physiological distinction, the discovery of which, by Sir Charles Bell, in the early part of this century, has been regarded as the most important acquisition of physiology since the time of Harvey. Bell determined by experiment that the posterior roots are appointed for sensory, the anterior roots for motor, work. Thus both structure and function suggest that the spinal nerve is not *one* nerve, but two nerves united; and this point is settled beyond dispute, first, by the independent and unlike development of the two roots, and second, by their complete and permanent separation in such fishes as *Amphioxus* and *Petromyzon*. Each segment of the trunk may therefore be said to have two pairs of nerves, a sensory pair with ganglia, and a motor pair without ganglia.

Now we come to a question of absorbing interest not only to the embryologist but also to the anatomist and physiologist. Are the metameric arrangement, the division of labor or function, and the mode of development, essentially the same for the cranial as the spinal nerves? The several inquiries into which the question resolves

itself have not yet been fully answered ; but the investigation of the last ten years has heaped up affirmative evidences until the final answer has been in the main anticipated. Although a Dutch embryologist, Van Wijhe, has shown that Bell's law must be modified for the cranial nerves, yet we know from the researches that started with His, Balfour, and Marshall, that these nerves follow the same general law of development as the spinal nerves. We find posterior nerves with ganglia and anterior nerves without ganglia ; and the latter are purely motor as in the trunk, while the former are sensory. Some of these posterior cranial nerves, however, are mixed nerves ; that is, they have in addition to the regular sensory fibres motor fibres, and in this respect they appear to depart from the spinal nerve type. But this difficulty, which still remains to be cleared up, loses its force as an objection, when placed beside an overwhelming amount of evidence in favor of the homology of the two sets of nerves. The posterior nerves of the head and trunk have the same origin ; and the early development runs so exactly parallel in both cases, that their fundamental equivalence can no longer be seriously questioned. The cranial ganglia, according to the researches of Beard, receive, secondarily, some elements that are not added to the spinal ganglia ; but homologies are settled by original conditions, not by adventitious differences, and hence no objection can be raised on this score to the identification of the nerves. That the cranial nerves agree with the spinal in having a metameric arrangement is made evident by their relations to undoubted segmental structures of the head, such as the gill-arches and the head-cavities.

I must now invite you to the very borders of the beaten ground of investigation; and I hope you will have the fortitude to follow me even to the brink of a precipice or two, should it be necessary, in order to get a view of the steep ascent which now challenges further advance in this direction. I have endeavored to give you the salient points in the historical development of the subject, and it remains for me to define the position now occupied, and so far as possible, by way of anticipation, the path which investigation is destined to take in the immediate future.

In the anterior region of the head, into which the cordal axis or "primitive backbone," as Lankester has called it, does not extend, there are two sensory nerves, the olfactory and the optic, which investigation has thus far failed to reduce to the type of the spinal nerves. No corresponding motor nerves exist; and no decisive evidence of metamerism has yet been discovered in their development, or adult condition. Foremost authorities in anatomy and embryology, like Gegenbaur, Balfour, and Kölliker, have declared that here a dividing line must be drawn, separating the head into two distinct regions, one of which bears with the trunk the common stamp of metamerism, while the other is built upon a plan of its own. It is here that Balfour, looking back into the remote ancestral history of the vertebrates for clews, recognized what appeared to him a primitive boundary line, corresponding to what now divides the head and trunk in many invertebrate forms. According to this view, the fore-brain would represent the *whole* of the ancestral brain, while the mid-brain and hind-brain would represent a number of segments belonging origi-

nally to the trunk, but now pressed into the service of the head. This conversion of trunk into head, in answer to the greater and greater demands made upon the brain, as the vertebrate line rose in the scale of development, is just that kind of economy which nature everywhere practises, and which we find exhibited in most instructive grades of elaboration in the nervous system of invertebrates. That this has been the history of the mid and hind portions of the vertebrate brain, is a truth resting upon so many convergent lines of evidence that there is no longer room for scepticism.

The fore-brain, in which the problem culminates, is still enveloped in a dense cloud of uncertainty, pierced by so few and feeble rays of light that we are compelled to accept the lead of conjecture, or to abandon the hope of further advance. We are limited to three hypotheses : We may assume with Balfour, that the fore-brain is the unsegmented brain inherited from an invertebrate ancestor ; or with Kölliker, that it is a new formation, representing an outgrowth from the unsegmented anterior end of the primitive nervous axis ; or with Kleinenberg, that it represents a number of fused trunk segments, in which the ancestral brain—the “head-ganglion” of annelid worms—has either been absorbed beyond the hope of identification, or totally suppressed.

Balfour's view marks the level of investigation ten years ago. Since that time the progress of discovery has been steadily in the direction of Kleinenberg's view. But we have reached a point where direct, demonstrative evidence appears to vanish, and it is only by the circuitous route of circumstantial evidence that we can push onward. The solution we are looking for does not lie

in the skull, the primordial cranium, the cranial nerves, the head-cavities, or the gill-clefts, nor, in short, in any one organ or system of organs that could be named in the head. As Professor Dohrn has insisted, both by word and example; nothing less than a complete analysis of the whole head and trunk can furnish a safe foundation for speculation on this subject. But the task does not end with the vertebrates. The present vertebrate head represents the cumulative development of unnumbered æons, and its ancestral history is only very imperfectly recorded in its embryonic development. Our analysis must therefore be extended to the worms, the arthropods, the molluscs, and, as it now appears, even to the coelenterates. The history of metamerism must be traced upwards, and the lessons of the simpler types must be our stepping-stones to a knowledge of the higher.

There is little prospect of ever knowing precisely how many segments the ancestor of the vertebrates possessed. The number varies in the different branches of a common stock ; and we know that this variation is the result of loss in many cases, and suspect that it may be due to addition in others. But we know that this variability in number has very definite limitations in the laws that control the formation of segments. The possibilities in this respect are by no means the same for all regions of the segmented axis. Although the head segments have undergone the greatest modifications in form, *fixity in number is here the rule*, while variation, if we except degenerate forms, is confined to the posterior trunk segments. In the embryo the anterior segments are invariably first in formation,

and generally so in definition, the addition of new segments taking place from behind. *There is not the least ground for supposing that a single segment has ever been, or can ever be, added to the anterior end.* If, in the course of development, segments disappear, the loss is borne by the posterior end, as we see when the tadpole lays aside its fish-like tail in rising to the estate of frogdom. The direction of loss is the reverse of that of acquisition, the one travelling away from, the other towards, the head. Thus the point of maximum variability in number is always most remote from the head. Both the laws of development and the conditions of continued existence tend to strengthen the distinction. The head segments developing first, have the advantage in the struggle for existence, and their supreme importance is the guarantee of their permanence.

Although there is not the least probability, and scarcely a possibility, of adding or interpolating entirely new segments in the head region, and although the chances of loss appear to come to a vanishing point a long way behind this region, still the shadow of uncertainty is not dispelled, and we have to acknowledge that we do not yet know how far the transforming influence of functional changes and substitution of organs has here been felt.

In looking around us for a possible foothold, we inquire, first of all, if there are not some structures connected with the fore-brain on which the seal of metamerism has left an indelible impression. One pair of these so-called cerebral nerves, the olfactory, have fast been losing their high claims to a position of isolation,

until at last, stripped of one disguise after another, they have been almost, if not quite, reduced to the level of the sensory nerves of the trunk and hind head, through the researches of Marshall, His, Beard, and others. The identification of this pair of nerves with the rest of the segmental sensory nerves, on the basis of development and structural features, is a triumph of investigation so near at hand that it is scarcely premature to proclaim it. The chain of discoveries bearing on this subject has still many links to be supplied, and here is one of the opportunities of the hour.

The optic nerves still hold undisputed possession of the very pinnacle of isolation ; and even to question their claim to such a position may appear to betray a woful superabundance of speculative audacity that would be less unbecoming to a romancing visionary than to the sober investigator. But without hesitation or misgivings, and without any special claim to scientific precision, I venture to predict that these nerves and their sense-organs will yet fall into line with the other sense-nerves and sense-organs.

I cannot here enter very far into the question of the origin of the vertebrate eyes, but the subject is one of such great interest, that, at the risk of overtaxing your forbearance, I venture to ask your indulgence for a few general remarks. The evidence in favor of the derivation of the organs of the special senses from a common basis, has been growing during the past few years with such astonishing rapidity, that the hypothesis of independent origin has no longer a respectable claim to attention. If the eyes have been derived from some simpler form of sense-organs possessed by the ancestors

of the vertebrates, we can only expect to find out what those primitive organs were by searching among invertebrate animals of the ancestral type. By common consent we turn to the annelids, or segmented worms. Here we find sense-organs of a low order, segmentally arranged, and supplied by nerves bearing ganglia, which correspond in position and general relations to the spinal ganglia of vertebrates. That the segmental nerves and ganglia of the annelids are the morphological equivalents of the spinal nerves and ganglia of vertebrates, is a proposition that now admits of little doubt. If the argument holds for the nerves and ganglia, the basis is given for the comparison of sense-organs. But are there any sense-organs in the vertebrates that can be said to agree in structure and function with the segmental tactile organs of annelids? Leydig and Eisig have given an affirmative answer to this question, and their views have already met with general acceptation. The sense-organs of the lateral line of fishes and amphibia, rudiments of which have been found by Froriep and Beard in the higher classes of vertebrates, have essentially the same structure, the same or a closely allied function, and, so far as known, fundamentally the same mode of development.

Allowing then that these organs are the homologues of the segmental sense-organs of annelids, there arises the very important question, is it possible for such organs to develop into those of the special senses, taste, smell, sight, and hearing? In the vertebrates we meet with no serious difficulty until we come to the eye. The sensory impressions received by a visual organ differ so radically from those received by a tactile organ, that it seems

almost incredible that cells devoted to one of these functions could ever serve the other. Nevertheless, this marvellous transformation and change of function have actually taken place, and the fact still admits of ocular demonstration in a very large group of annelids. Sometimes all the tactile cells are converted into visual cells; at other times only a part of the cells assume the new function, while the rest continue to serve the old. The result is that we have at one end of the series pure visual organs, at the other end pure tactile organs, and between the two extremes every grade of mixture represented in veritable compound sense-organs. The picture is a revelation that gives swift wings to suggestion. If such is the path of evolution in one case, the best ground is given for suspecting that the same economy has been practised elsewhere. The discovery of these facts in the leeches, led naturally to the anticipation of a similar origin for the eyes in other annelids and in those groups that have had a common origin with the annelids, before all the arthropods and vertebrates. The existence of segmental sense-organs, as I have said, is well known in other annelids than the leeches, and the origin of eyes from them is fairly well indicated in many cases. It is a most promising subject of investigation, which, like a thousand others, still waits for the encouragement which the wealth of this country will not long, I trust, refuse to supply.

The close relationship between the annelids and arthropods rendered it probable that in the latter the eyes were also derived from segmental sense-organs, and the probability was strengthened by the arrangement of the eyes in successive pairs, as in the larvae of many insects.

My anticipations seem to have been in the right direction, so far as I can judge from the observations of Dr. Patten, which have been carried on during the last three years through the generous support of Mr. Allis, of Milwaukee.

So far then, as we now understand the genesis of sense-organs, both in the vertebrates and in the invertebrates, the evidence all points to the derivation of the paired eyes of vertebrates from segmental sense-organs. The development of the vertebrate eyes has never been studied from this stand-point; but the subject is a most inviting one, and offers a broad field for observation and reflection.

The existence of an unpaired median eye in vertebrates, which has been claimed by a number of recent investigators, is rendered doubtful by Professor Leydig's careful researches. If the pineal organ turn out to have been a visual organ, it will present a difficulty not easy to dispose of on the hypothesis of derivation from segmental sense-organs. All such sense-organs are *paired*, and a single median eye could arise from them only through the fusion of at least one pair of eyes. We have examples of such fusion in the invertebrates; but it might be extremely difficult to find any evidence favoring a double origin of the pineal organ. Investigation must lead with a searching analysis of structure and development in every group of vertebrates, while keeping up the search for a homologous structure in the invertebrates.

We have now followed the subject of the metamerism of the vertebrate head far enough to get a clear idea of its essential features and general bearings. We started

with a special problem and found it to be the centre of inquiries, leading in all directions into the unknown. So it is with all special subjects in biology. The farther we pursue them the broader and more interesting they become. Nothing could be farther from the truth than the idea that such questions are isolated, and devoid of interest to all except the specialist.



